The brain of *Micropotamogale lamottei* Heim de Balsac, 1954

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Abstract

Studied the brain of *Micropotamogale lamottei*. It differs markedly from the brains of "average Insectivora" by less developed olfactory structures and a larger medulla oblongata. The large size of the latter is caused by a marked enlargement of the nucleus of the spinal trigeminal tract. Since similar characteristics are present in all water-adapted Insectivora, such as *Limnogale, Potamogale, Neomys, Desmana,* and *Galemys,* they are thought to be related to predatory habits in limnetic ecosystems. The trigeminal system, innervating the strongly developed vibrissae of the muzzle, is thought to replace the olfactory system in water-adapted Insectivora and to become the main sensory system involved in searching for food. Within the otter-shrews, the enlargement of the medulla oblongata and the concomitant reduction of the olfactory structures are in *M. lamottei* less marked than in *Potamogale velox.* Similarities in the brain characteristics of *M. lamottei* are with the shrew-like tenrecs of Madagascar (Oryzorictinae).

Introduction

The african water or otter-shrews comprise two genera (*Micropotamogale* and *Potamogale*) and three species (*M. lamottei, M. ruwenzorii,* and *P. velox*) from which, so far, only the brain of the giant form *(P. velox)* has been investigated (Stephan and Spatz 1962; Bauchot and Stephan 1967, 1968, 1970; Stephan 1967; Stephan and Andy 1982). The brain of *P. velox* was found to have several characteristics which set it apart from most other Insectivora brains investigated. These are: 1. the tremendous size of the medulla oblongata, caused mainly by the extraordinary development of the nucleus of the spinal trigeminal tract; and 2. relatively very small structures of the main olfactory system. These special features of *P. velox* are obviously related to its search for food in water, and it would be of interest to know if similar brain characteristics are present also in the dwarf otter-shrews of the genus *Micropotamogale.* This paper focusses on four problems:

1. Are there brain characteristics common to *Potamogale* and *Micropotamogale* which set the brains of these otter-shrews apart from those of other Tenrecidae and other Insectivora families?
2. Can these brain characteristics be related to the search for food in water and do they exist in *Micropotamogale* to the same degree as they do in *Potamogale*?
3. On the basis of brain development, what is the general evolutionary level of otter-shrews with respect to other Insectivora, and what is their status with respect to each other?
4. Are the results compatible with the classification of otter-shrews?

Material and methods

The description of the macromorphology of the brain of *M. lamottei* is based on two brains (320, 1728). For the determination of brain size, the cranial capacities (CrC) of four skulls were measured and, in addition, twelve skulls of *P. velox* and three skulls of *M. ruwenzorii* were also measured.

Volumes of the brain parts were determined from three frontally serial-sectioned brains (320, 1227, 1728) of *M. lamottei.* Corresponding volumes of two brains of *P. velox* (A 240, A 367) and of 26 other species of Insectivora (incl. 2 species of Macroscelidea) were used for comparison. Data on these volumes were published by STEPHAN (1967), and STEPHAN et al. (1970, 1981).

The brain components investigated so far are: medulla oblongata, cerebellum, mesencephalon, diencephalon, and telencephalon; and within the telencephalon: olfactory and accessory olfactory bulbs, piriform lobe (= palaeocortex + amygdala), septum, striatum, hippocampus, schizocortex, and neocortex.

The methods of volume determination as well as volume (and brain weight) comparison were described in detail in previous papers (mentioned above) and so only brief comments need be given now. Firstly, all volumes are corrected to the fresh brain, and secondly, the comparisons are based on the allometric method.

By aid of the allometric method the interdependency of body weight on one hand and brain weight or volume of various brain parts on the other hand was determined by calculating regression lines within groups of closely related mammals, usually families or subfamilies. In the double logarithmic scale the regression lines of these groups have remarkably uniform slopes, even if the groups belong to different orders of mammals. By a canonical averaging method, for the mathematical basis of which we are indebted to Dr. U. REMPE from the University in Kiel (Germany), the common slope has been derived using data from 34 groups within Insectivora, Primates and Chiroptera. This slope is 0.66 for the total brain (Fig. 7) and between 0.53 and 0.73 for the various brain parts (Figs. 9–11). A reference line with the slopes thus derived can be drawn anywhere in the double logarithmic diagrams. Since we are interested in this paper in comparing the otter-shrews with other Insectivora, the reference lines were plotted through the average log body weight and the average log brain weight or log volume of brain structures of the 28 species of Insectivora and Macroscelidea studied. Any value on this line will be considered in the following presentation to represent the "average Insectivora". The distance of *M. lamottei* (as well as that of *P. velox* or any other species) from the reference line expresses the degree of deviation from the "average Insectivora". When measured parallel to the ordinate and given in antilogs, such values express immediately the size of the given structure relative to that of an "average Insectivora" of equal body weight. The reference line itself has of course a distance of 0, the antilog of which is 1 (or = 100 %). Parallel lines, drawn in Figures 7 and 9–11 in multiples of 0.301 (which is the logarithm of 2), show when a doubling or quadrupling or when a half or a quarter is reached. We have called such values "indices of comparison" (allometric indices, progression indices, enlargement factors). In Figures 8, and 13 to 16, the indices have been scaled.

The structure which has undergone the greatest enlargement in primate evolution is the neocortex (STEPHAN 1972). Consequently neocortical size can be expected to represent the best cerebral criterion (at present available) for the evolutionary level of a given species. In Figures 8, 13, 14 and 15 the vertical columns (= range of variation) of the systematic (taxonomic) groups were arranged from left to right according to increasing neocortical indices as shown in Figure 16. The same arrangement is present in all scales and so the trends in the data can be easily seen, as can the relationships of the brain components of otter-shrews to those of other Insectivora.

Results

Macromorphology

In the brain of *M. lamottei,* the olfactory bulbs clearly project beyond the frontal poles of the hemispheres and are relatively broad. In the dorsal view (Fig. 1), a very small part of the mesencephalon is visible between telencephalon and cerebellum. Each cerebral hemisphere is wedge-shaped and its largest width is found in the caudal third. From the side (Fig. 2), the brain appears relatively flat. From below (Fig. 3), a very big trigeminal nerve as well as a very big medulla oblongata are conspicuous. The flocculi are well developed.

Compared with *P. velox* (Figs. 4–6), the hemispheres and the olfactory bulbs of *M. lamottei* are shorter and broader. In the dorsal view, the caudal borderline of each hemisphere is pointed in *P. velox* (Fig. 4), but broad and rounded in *M. lamottei.* The angle between the caudal contours of the two hemispheres is 105° and 155°, respectively. In *P. velox,* the gap is filled by the cerebellum, and especially by its vermis, whereas in *M. lamottei,* a small cleft separates telencephalic hemispheres and cerebellum. Apart from these differences, the brains of *M. lamottei* and *P. velox* are similar in their macromorphological appearance.
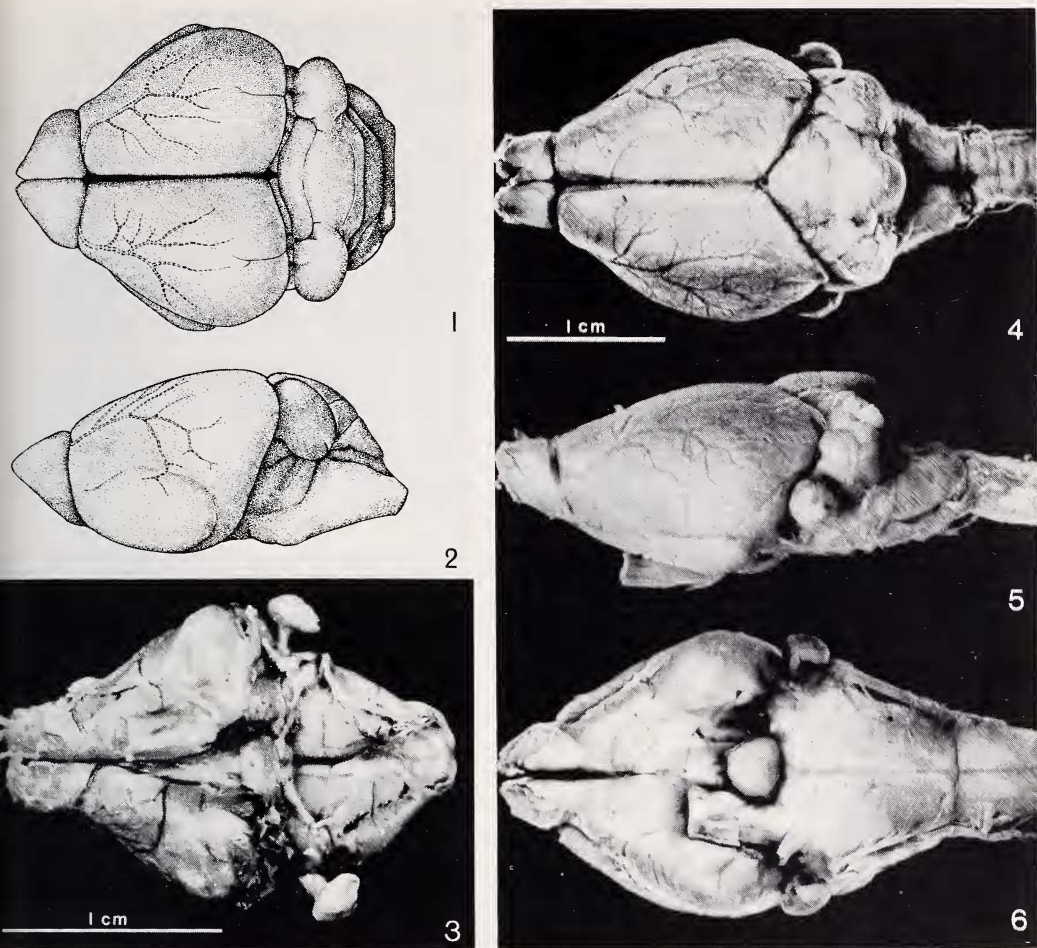
Figs. 1–3. Brain of *Micropotamogale lamottei* from dorsal side *(Fig. 1),* left side *(Fig. 2),* and ventral side *(Fig. 3).* Linear enlargement 3,0 x. The drawings (Figs. 1 and 2) are made from brain 494 by H. J. KUHN, the photograph (Fig. 3) is taken from brain 1728. The latter brain was fixed in situ and not prepared and photographed until two weeks later. By that means the peduncles of the cerebellar flocculi are stretched. – Figs. 4–6. Brain of *Potamogale velox* (A 240) from dorsal side *(Fig. 4),* left side *(Fig. 5),* and ventral side *(Fig. 6).* Linear enlargement ca. 2.15 x

Brain size and encephalization

Brain and body size

For interspecific comparisons using the allometric method, data on body size and brain size are needed. Data on body weights are rare but are available for all three species of otter-shrews. Brain weights are available only for *P. velox.* For the two species of *Micropotamogale,* fresh brain volumes were determined indirectly from cranial capacities (CrC) and from the volumes of serially sectioned brains (VSS). CrC measurements in twelve skulls of *P. velox,* four of *M. lamottei,* and three of *M. ruwenzorii* were made by introducing fine dust shot into the cranial cavity through the foramen magnum, weighing the skull before and after introducing the dust shot, and by dividing the weight difference

Table 1

Body weights, brain weights, cranial capacities and serial section volumes in otter shrews

Species	Protocol number	Sex	Body weight g	Brain weight measured mg	Cranial capacity measured mm³	Serial section volume measured mm³	Brain weight determined mg	Origin of material
Micropotamogale ruwenzorii	31042	f	–	–	1,079	–	1,201	skull, Mus. Tervuren
	31466	f	–	–	1,140	–	1,269	skull, Mus. Tervuren
	31719	u	–	–	954	–	1,062	skull, Mus. Tervuren
	9078	f	90	–	–	–	–	RAHM (1960)
	9079	f	80	–	–	–	–	RAHM (1960)
	10288	f	75	–	–	–	–	RAHM (1960)
	?	u	135	–	–	–	–	RAHM (1961)
mean			95 (n=4)		1,058 (n=3)		1,177 (n=3)	
Micropotamogale lamottei	494	m juv	–	–	–	(235)	–	brain, coll. KUHN
	1227	m	60	–	–	357	718	brain, coll. KUHN
	1728	f	70.6	–	–	452	908	brain, MPI, VOGEL via BAUCHOT
	320	m	68	–	746	–	830	skull, coll. KUHN
	2273	f	53 (ca)	–	693	–	771	skull, coll. KUHN
	?	m	–	–	769	–	856	skull, LAMOTTE via BAUCHOT
	2329	m	–	–	668	–	743	skull, coll. STARCK
	?	m	–	–	–	–	–	VOGEL, pers. comm.
mean			64.2 (n=5)		719 (n=4)	405 (n=2)	804 (n=6)	
Pomatogale velox	A240	m	780	4,700	–	–	–	brain, coll. MPI
	A345	m	743	4,500	–	–	–	brain, coll. MPI
	A357	m	668	4,100	–	–	–	brain, coll. MPI
	A365	f	592	3,820	–	–	–	brain, coll. MPI
	A367	m	517	3,700	–	–	–	brain, coll. MPI
	626	u	–	–	3,936	–	4,381	skull, Mus. Tervuren
	1593	u	–	–	4,109	–	4,573	skull, Mus. Tervuren
	3221	u	–	–	4,168	–	4,639	skull, Mus. Tervuren
	4198	u	–	–	3,626	–	4,034	skull, Mus. Tervuren
	7063	u	–	–	3,431	–	3,819	skull, Mus. Tervuren
	7202	f	–	–	3,850	–	4,285	skull, Mus. Tervuren
	12318	m	–	–	4,219	–	4,696	skull, Mus. Tervuren
	12319	f	–	–	3,544	–	3,944	skull, Mus. Tervuren
	14158	m	–	–	3,634	–	4,045	skull, Mus. Tervuren
	15889	u	–	–	3,368	–	3,749	skull, Mus. Tervuren
	18974	m	–	–	3,665	–	4,079	skull, Mus. Tervuren
	25500	f	–	–	3,339	–	3,716	skull, Mus. Tervuren
mean			660 (n=5)	4,164 (n=5)	3,741 (n=12)		4,163 (n=12)	

by 5.6121, which was found to be the weight in grams per cubic centimeter dust shot. The results are given in Table 1, column 5.

Both brain weights and cranial capacities are known only for *P. velox*. Based on the average values of the two parameters (Table 1, columns 4 and 5) a conversion factor (C_{CrC}) was calculated.

$$C_{CrC} = \frac{\text{average brain weight}}{\text{average cranical capacity}} = \frac{4,164}{3,741} = 1.113$$

The same calculation was made using the maximal brain weight given in column 4 and the maximal cranial capacity given in column 5 ($= \frac{4,700}{4,219} = 1.114$) as well as using the minima ($= \frac{3,700}{3,339} = 1.108$). Thus 1.113 can be considered to be an appropriate factor for converting cranical capacities to brain weights in *P. velox*.

This factor was also used to convert the cranial capacities of the two species of *Micropotamogale* to brain weights. This could introduce some inaccuracy in the calculation, but it could be checked in *M. lamottei* by another approach in which the volumes were calculated from serial-sections. In more than 300 brains of insectivores, primates and bats, in which both the fresh weights and the serial-section volumes were measured, we found that the average relationship between these two parameters (C_{VSS}) was 1.94 · 1.036 (STEPHAN et al. 1981). 1.036 is the specific gravity of fresh brains and so can be used to convert brain volumes into brain weights or vice versa. 1.94 is the average shrinkage in brain volume due to fixation and embedding procedures. With $C_{VSS} = 2.01$ the serial-
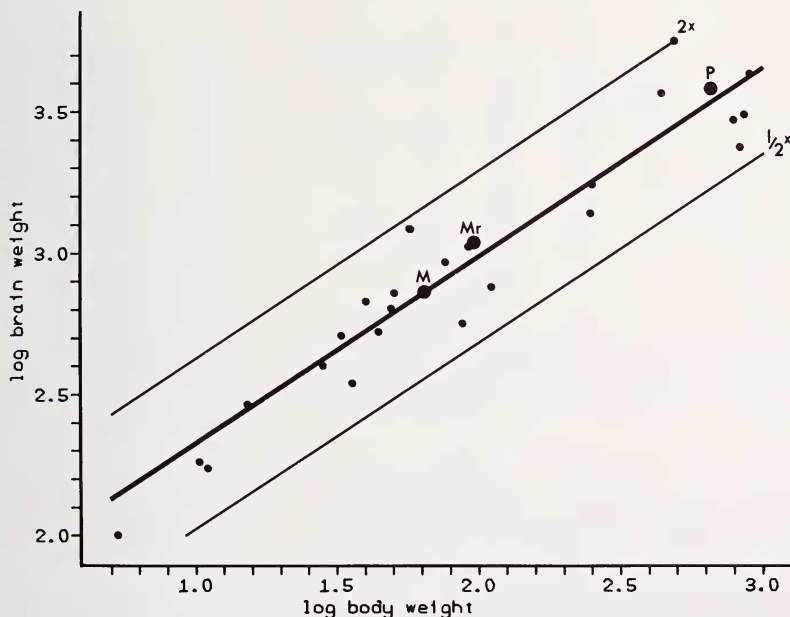

Fig. 7. Brain weight (in milligram) plotted against body weight (in gram) in a double logarithmic scale. The reference base-line (thick) has a slope of 0.66 and is plotted through the average log brain weight and the average log body weight of 26 Insectivora and 2 Macroscelidea species. Its formula is: log brain weight = 1.708 + 0.66 · log body weight. The thinner parallel lines point to deviations according to the factor 2, i.e. two times (= 200 in Fig. 8) or one-half time. The three otter-shrew species are marked by big round dots. M = *Micropotamogale lamottei*, Mr = *Micropotamogale ruwenzorii*, P = *Potamogale velox*. (For further explanations see 'Material and methods')

section volumes of the two brains (1227, 1728) of *M. lamottei* (Table 1, column 6) were converted to fresh brain weights (column 7). The average (813 mg; n = 2) is very close to the average obtained from the CrC measurements (800 mg; n = 4) when using $C_{CrC} = 1.113$. The overall average is 804 mg (n = 6) (Table 1). The brain of the juvenile animal 494 is clearly smaller and therefore was not taken into account. This animal still had all of its milk-teeth, i.e. its first dentition (KUHN 1964).

Encephalization

The data in Table 1 indicate the following provisional standards of body and brains weights in the otter-shrews: *M. ruwenzorii* 95 g/1,180 mg, *M. lamottei* 64.2 g/800 mg, and *P. velox* 660 g/4,160 mg. These standards result in encephalization indices of 115, 101 and 112, respectively, the average of which is 109 (Fig. 8). Thus, the weight of the brain in otter-
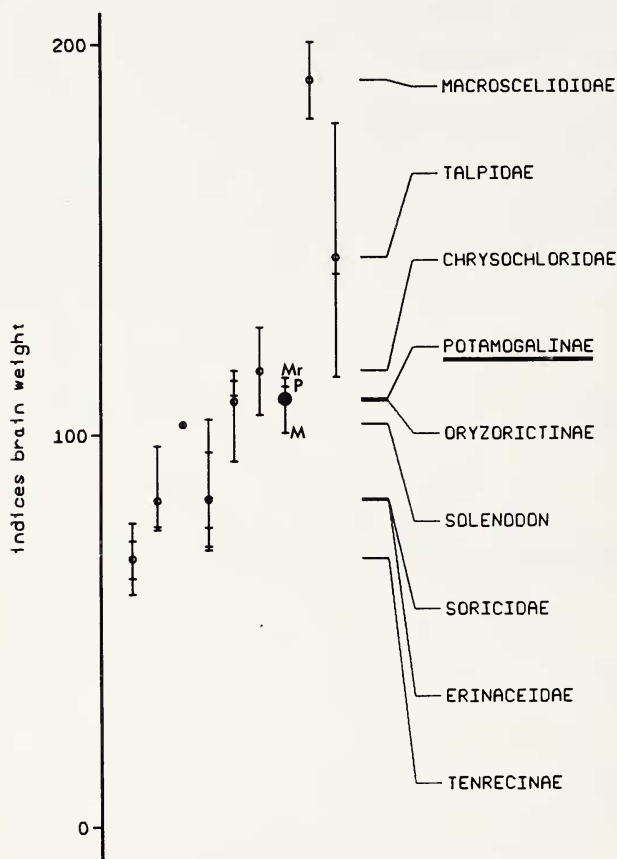

Fig. 8. Brain weight (encephalization) indices. The indices are numerical values of the distances from the base-line in Fig. 7 and given in percent. The base-line represents the "average Insectivora" and is 100 %. Vertical bars represent the range of variation within each systematic group (families or subfamilies) with the average marked by a dot. The bars are arranged from left to right according to increasing neocortical progression (taken from Fig. 16). The three otter-shrew species are marked as in Fig. 7. The horizontal bars to the right correspond with the mean of the individual systematic group, the name of which is given. (For further explanations see 'Material and methods')

shrews is about the same as that in the "average Insectivora" (= 1 or 100 %) or slightly larger. As far as can be ascertained from the poor material available, the encephalization of *P. velox* and *M. ruwenzorii* is somewhat higher than that of *M. lamottei*.

As can be seen from Figure 8, otter-shrews and the Oryzorictinae (the shrew-like tenrecs of Madagascar) have an equal degree of encephalization. Higher indices are found in the Macroscelididae and Talpidae, lower ones in the Erinaceidae, Soricidae and especially in the hedgehog-like tenrecs of Madagascar (Tenrecinae). The lowest index in

Insectivora was found to be 60 in *Tenrec ecaudatus*. Allometric comparisons indicate that the brain of *M. lamottei* is 1.7 times larger and those of *M. ruwenzorii* and *P. velox* are 1.9 times larger than that of *Tenrec*. When compared with the corresponding scale for the neocortex (Fig. 16), the encephalization (= total brain) indices of the otter-shrews (Fig. 8) are low. As will be shown in the following paragraphs, this is due both to a relatively large neocortex and to especially small non-neocortical portions of the brain, particularly the olfactory structures.

Composition of the brain

The *average volumes* of the various structures of *M. lamottei*, and the standard errors of the mean (SEM) in percent of the mean, are given in Table 2 (columns 1 and 2, respectively). Within *M. lamottei*, the greatest variation in size occurred in olfactory bulbs, cerebellum, and septum, the lowest in the diencephalon. The differences in variability of

Table 2

**Data on brain composition in otter shrews**

Structural complexes	Average volumes (mm³) in M. lamottei (n=3)	SEM (%)	Percentage composition of the total brain (net tissue = 100 %)				Allometric indices related to Insectivora regression lines (= 100 %)		
			M. lamottei	P. velox	Average of the two species	Average of 26 Insectivora and two Macroscelidea species	M. lamottei	P. velox	Average of the two species
Medulla oblongata	134.9	14.7	18.2	19.5	18.8	12.9	141	205	173
Cerebellum	82.7	18.7	11.1	15.6	13.4	13.2	87	125	106
Mesencephalon	58.6	8.5	7.9	6.5	7.2	6.3	123	154	139
Diencephalon	62.8	2.3	8.4	7.7	8.1	7.7	111	118	115
Telencephalon	404.1	6.5	54.4	50.7	52.5	59.9	91	95	93
Bulbus olfactorius	34.1	24.1	4.6	2.3	3.4	8.4	57	39	48
Palaeocortex	67.3	13.9	9.1	5.0	7.0	15.2	61	47	54
Septum	15.1	17.4	2.0	1.3	1.7	1.7	119	107	113
Striatum	32.6	6.4	4.4	3.5	3.9	5.0	90	79	85
Schizocortex	32.9	10.6	4.4	3.7	4.1	3.6	127	129	128
Hippocampus	77.7	7.2	10.5	7.7	9.1	9.3	112	114	113
Neocortex	144.4	6.1	19.4	27.2	23.3	16.7	125	167	146

the various components seem to be mainly due to true intraspecific variation rather than to difficulties in the delineations. Structures difficult to delineate, as for example diencephalon and mesencephalon, have lower SEM-values than those easy to delineate (olfactory bulbs, cerebellum). Similar results were obtained from data of 165 brains of Insectivora and Primates (STEPHAN et al. 1981).

The *percentages* of the measured brain components relative to the net volume of the total brain (= 100 %) are given in column 3 of Table 2. Compared with corresponding values of *P. velox* (column 4), the cerebellum of *M. lamottei* is relatively small, and the telencephalon relatively large. Within the telencephalon, the olfactory bulbs, the palaeocortex, and the hippocampus are larger in *M. lamottei* than in *P. velox*, whereas the neocortex is distinctly smaller.

Compared with the average percentages of brain components in 26 Insectivora and 2 Macroscelidea species (column 6), the otter-shrews, on the average (column 5), have a clearly larger medulla oblongata but a smaller telencephalon. Within the telencephalon, the percentages of olfactory bulbs and palaeocortex are clearly smaller in the otter-shrews, whereas the neocortex is distinctly larger.

Since the percentages of the various structures are not independent of one another (e.g.
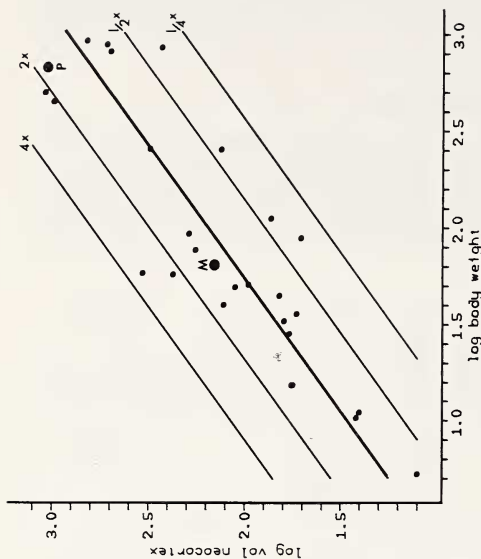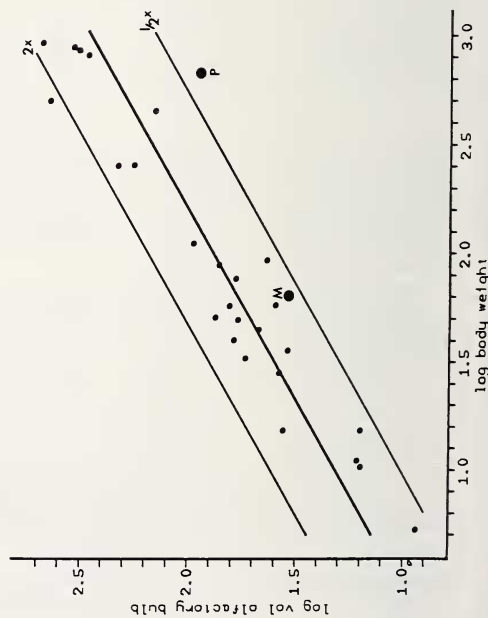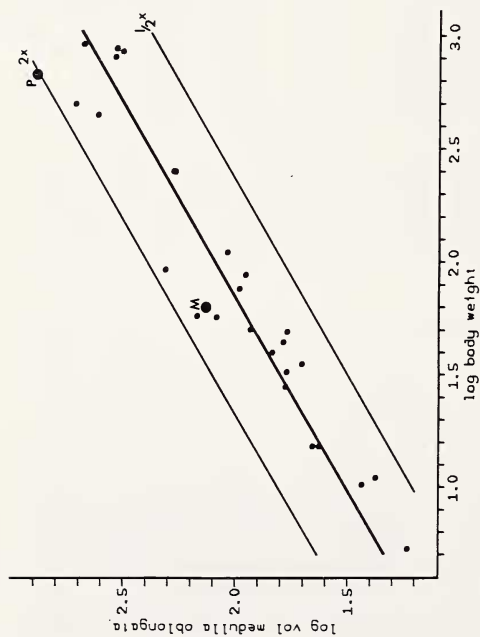
Figs. 9–11. Volume of brain structures (in mm³) plotted against body weights (in gram) in double logarithmic scales. *Fig. 9:* medulla oblongata; *Fig. 10:* bulbus olfactorius; *Fig. 11:* neocortex. Reference base-lines (thick) are through the point of the average volume of each structure and the average body weight of 26 Insectivora and two Macroscelidea species. Their formulas are:

log volume medulla oblongata = 0.93 + 0.58 · log body weight
log volume olfactory bulb = 0.74 + 0.57 · log body weight
log volume neocortex = 0.74 + 0.73 · log body weight.

The deviation indices are given in Figs. 13, 14 and 16, respectively. The two otter-shrew species are marked by big round dots. M = *Micropotamogale lamottei*, P = *Potamogale velox*. (For further explanations see Fig. 7 and Material and methods¹)

the high percentage for the medulla oblongata will tend to reduce the percentages for all other brain parts) the volumes will also be compared by the allometric index method.

The *allometric indices* of the various brain parts of *M. lamottei* indicate the deviation of this species from an "average Insectivora" of equal body weight. In Figures 9 to 11, the sizes of the indices correspond to the distances of the big dots marked M from the thickly-drawn lines. They are close to 100 when the structure under consideration is of similar size to that of an "average Insectivora", and some distance from 100 when the structure varies in size from an "average Insectivora". In Figure 12, we have summarized the indices of all measured structures for both *M. lamottei* and *P. velox*.

In both species, the highest deviation from the "average Insectivora" is that of the accessory olfactory bulb, but the direction of deviation differs between the species. Whereas the accessory bulb is minute in *M. lamottei* (index = 28) it is especially large in *P. velox* (index = 276), i.e. nearly ten times larger (body size equalized). Similar differences, but by far less dramatic, are found in the cerebellum which, in *M. lamottei*, is smaller than in the "average Insectivora" (index = 87) but which, in *P. velox* is larger (index = 125). All other structures in the two species deviate in the same direction from the "average Insectivora". Especially large, and comparatively larger in *P. velox* than in *M. lamottei*, are medulla oblongata (indices = 205 versus 141) (Figs. 9 and 13), neocortex (167 versus 125) (Figs. 11 and 16), and mesencephalon (154 versus 123), whereas in both species similar indices are found for schizocortex (127 and 129), septum (107 and 119), hippocampus (114 and 112) and diencephalon (118 and 111) (Fig. 12).

The olfactory bulb is especially small both in *M. lamottei* and *P. velox* (Figs. 10 and 14) with indices of 57 and 39, respectively. Similarly low values are found for the olfactory cortices (palaeocortex) which, however, also contain the amygdala. The low values for the olfactory structures are
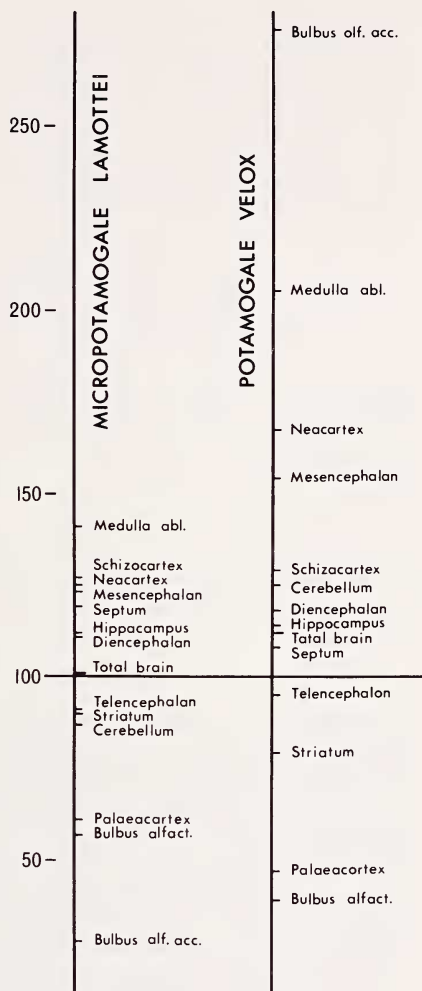
Fig. 12. Distances from the base-lines given in % of the average Insectivora (= 100) for the structures measured in *Micropotamogale lamottei* and *Potamogale velox*

considered to be one reason for the small size of the telencephalon as a whole, which in the otter-shrews is smaller than in the "average Insectivora", though the neocortex is clearly larger. Another reason for the small size of the telencephalon is the low value for the striatum in the two species (Fig. 15). The indices are 90 for *M. lamottei* and 79 for *P. velox* (Table 2 and Fig. 12).

Discussion

Brain characteristics of otter-shrews compared with those of other families of Insectivora

Similarities in macromorphology and composition of the brains of *M. lamottei* and *P. velox* make it possible to specify brain characteristics which are common to the otter-shrews and hence facilitate comparisons with the brains of other Insectivora families and/or sub-families as described by Stephan (1967), Bauchot and Stephan (1970), and Stephan and Andy (1982). Such brain characteristics, which either alone or in combination specify otter-shrew brains, are: 1. no exposure (or very little) of the mesencephalic tectum; 2. a gradual tapering of the medulla oblongata into the spinal cord, 3. the tremendous size of the medulla oblongata, and 4. the very small size of the structures of the main olfactory system.

The brains of the hedgehog-like tenrecs of Madagascar (Tenrecinae), of the golden moles (Chrysochloridae) and of the elephant shrews (Macroscelidea) differ clearly from those of the otter-shrews in having distinctly larger gaps between the cerebral hemispheres and the cerebellum so that a large portion of the mesencephalic tectum is visible. Furthermore the brains of all of these families, as well as those of the solenodons (Solenodontidae), hedgehogs (Erinaceidae) and most shrews (Soricidae), are characterized by relatively larger olfactory bulbs and centers. From the brains of the shrews (Soricidae) and moles (Talpidae), those of the otter-shrews clearly differ in the shape of the medulla oblongata. In the otter-shrews it tapers off gradually into the spinal cord, whereas in shrews and moles it narrows abruptly.

Otter-shrew brains are most like those of the shrew-like tenrecs of Madagascar (Oryzorictinae). In general, the brains of the latter differ in having larger olfactory structures and a smaller medulla oblongata, except for *Limnogale mergulus,* which is also water-adapted.

Water adaptation

In the otter-shrews the marked enlargement of the medulla oblongata is the result of a strong development of the nucleus of the spinal trigeminal tract. Also the trigeminal nerves are extremely large (Figs. 3 and 6). They innervate the strongly developed vibrissae of the muzzle, which are thought to be vibration receptors adapted for detecting prey (mainly crustaceans) under water. The trigeminal system is thought to replace the olfactory system in water-adapted forms, and to become the main sensory system in the search for food. The main olfactory system (excluding the accessory olfactory system) seems to be unqualified for such a function. It is well developed in all terrestrial Insectivora and has probably undergone reduction in the water-adapted forms.

Both features (i.e. enlargement of the trigeminal system and simultaneous reduction of the olfactory system) are found also in other species with a similar adaptation. Thus, the olfactory system is reduced also in *Limnogale* (Oryzorictinae), *Neomys* (Soricidae), *Galemys* and *Desmana* (Talpidae), (marked by ~ in Fig. 14), whereas the medulla oblongata in all of these forms is large or very large (marked ~ in Fig. 13).

In contrast to the main olfactory bulb, the accessory olfactory bulb seems to be unaffected by the animal's adaptation to water. This small bulb, which is well developed in *P. velox* (index 276), is, in *M. lamottei,* even more reduced than the main bulb (indices 28 versus 52). In a similar manner, *Limnogale, Neomys,* and the Desmaninae which are also predators in limnetic ecosystems, show no consistency in the sizes of the accessory bulb but rather show a variation that encompasses the complete range of size found in Insectivora. Marked differences in accessory bulb development between species of the same family are found in various Insectivora families (Stephan 1965, 1975).
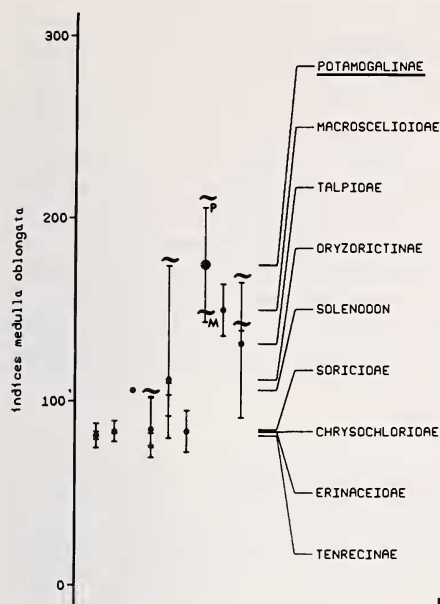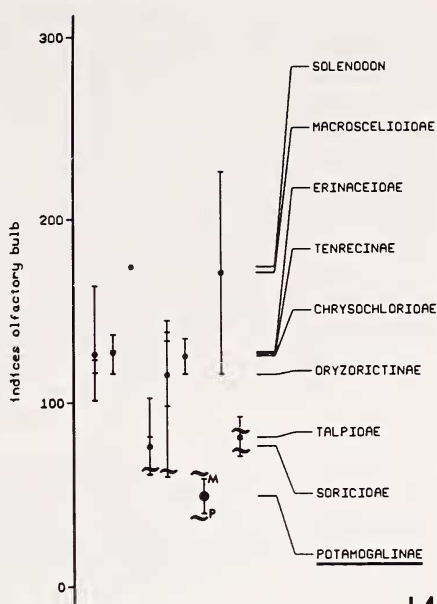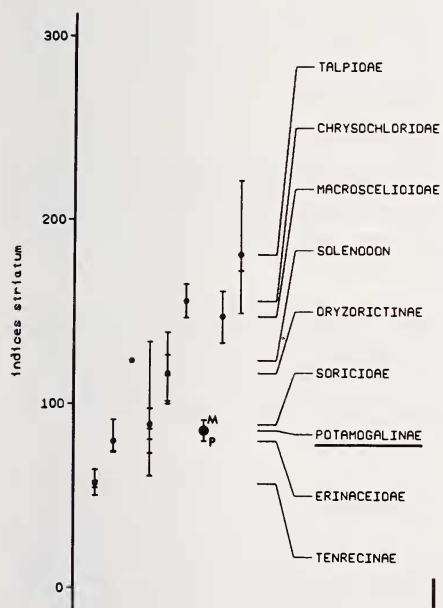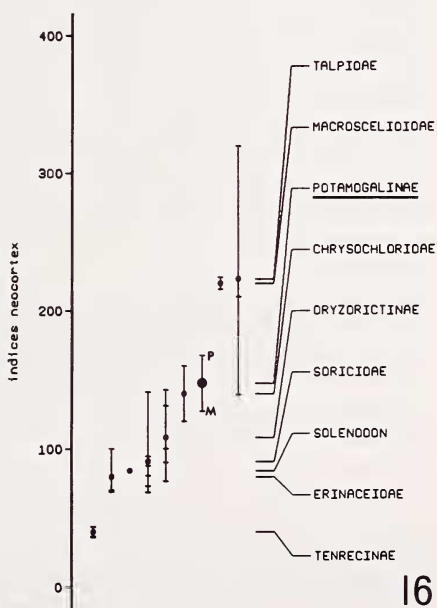
Figs. 13–16. Indices of the medulla oblongata *(Fig. 13)*, bulbus olfactorius *(Fig. 14)*, striatum *(Fig. 15)*, and neocortex *(Fig. 16)*. The indices are numerical values for the distances from the base-lines in Fig. 9–11, respectively, and given in percent of the "average Insectivora" (= 100). Species adapted to water are marked in Figs. 13 and 14 by ∼. (For further explanations see Fig. 8)

From the papers of Heim de Balsac (1954, 1956, 1957), Heim de Balsac and Bourlière (1955), Dewitte and Frechkop (1955), Guth et al. (1959, 1960), Rahm (1961) and Dubost (1965) *M. lamottei* is clearly less adapted to water than the other otter-shrews. *M. lamottei* has no laterally compressed tail, as does *P. velox,* and no webbed hands and feet, like *M. ruwenzorii.* There are, however, some indications that *M. lamottei* is also able to catch its prey in water. This species is found mainly in the vicinity of watercourses or of swamps, and crustaceans, which never leave water, were found in its stomach (Guth et al. 1959). The enlarged upper lip with its strongly developed vibrissae would, according to Guth et al. (1959, 1960), also suggest an adaptation to catching food in water.

The brain data support the suggestion that *M. lamottei* is less adapted to water than *P. velox.* In *M. lamottei* medulla oblongata and cerebellum are clearly smaller and the olfactory bulb is distinctly larger (Fig. 12). These structures (and others to a lesser degree) are more similar in size to those of terrestrial Insectivora. The larger size of the cerebellum in *P. velox* might be correlated with an adaptation to a large three-dimensional space as is found in their habitat, which is larger bodies of water.

The general evolutionary level of otter-shrews

When evaluated according to its encephalization (based on total brain size), the general evolutionary level of *M. lamottei* would be the same as that in the "average Insectivora" (index = 101), but when evaluated on the size of the neocortex, it is clearly higher (index = 125) (Fig. 12). The degree of development of the neocortex is probably the better criterion for estimating evolutionary levels.

According to its brain characteristics, *M. lamottei* is recognizably less progressive than *P. velox.* This is suggested by the somewhat lower indices of the total brain, the telencephalon as a whole and the diencephalon, and the clearly lower indices of medulla oblongata, mesencephalon, cerebellum, and especially of the neocortex. Some other brain parts have, in *M. lamottei,* somewhat higher indices than in *P. velox.* This includes the limbic structures (septum, schizocortex and hippocampus) and the main olfactory structures (main bulb and palaeocortex). However, these structures are of minor importance when evaluating the evolutionary level.

The general evolutionary level of the otter-shrews is considered to be in the upper half of the total range found in Insectivora, with *M. lamottei* closer to the "average Insectivora" and *P. velox,* and possibly also *M. ruwenzorii,* somewhat higher. The evolutionary level of *M. ruwenzorii* could only be estimated on the basis of its encephalization, since the brain itself and its composition could not be investigated. According to its encephalization, its place is closer to *P. velox* than to *M. lamottei.*

A lower position for *M. lamottei* and/or a higher one for *M. ruwenzorii* and *P. velox* were also found in anatomical and behavioral investigations by Heim de Balsac (1954, 1956), Guth et al. (1960), Verheyen (1961) and Dubost (1965). *M. lamottei* is considered to be closer to the basic forms than are the other two species; similarities with the shrew-like tenrecs of Madagascar (Oryzorictinae) are emphasized.

Classification of otter-shrews

Comments on animal classification based on brain characteristics generally must be regarded with care, since the brain's great plasticity frequently results in convergent developments (e.g. in water-adapted Insectivora). With these restrictions in mind, the brains of the otter-shrews are most like those of the shrew-like tenrecs of Madagascar (Oryzorictinae). This is true for the macromorphology of the brain, and for encephalization (based on comparison of total brain weights, Fig. 8), as well as for the allometric size of many structures, which have totally or partly the same range of variation in otter-shrews

as in Oryzorictinae. Such structures are: hippocampus, septum, cerebellum, schizocortex, telencephalon as a whole, neocortex, diencephalon, and medulla oblongata. In many respects *M. lamottei* is intermediate in brain composition between *P. velox* and the Oryzorictinae.

The results of our presentation are compatible with the view that the otter-shrews are so closely related to the tenrecs of Madagascar, that they should be regarded as a subfamily (Potamogalinae) of the Tenrecidae (CABRERA 1925, after FRECHKOP 1957; WEBER 1928). In support of these authors and contrary to SIMPSON (1945), who classified the otter-shrews as a separate family (Potamogalidae), the discovery of the dwarf otter-shrews induced HEIM DE BALSAC (1954) and HEIM DE BALSAC and BOURLIÈRE (1955) to reclassify the otter-shrews as a subfamily of the tenrecs. Later authors have supported this classification (GUTH et al. 1959, 1960; VERHEYEN 1961; RAHM 1961) and emphasized the intermediate position of the dwarf otter-shrews, and especially of *M. lamottei*, between Oryzorictinae and *P. velox*.

Acknowledgements

Zusammenfassung

Das Gehirn von Micropotamogale lamottei Heim de Balsac, 1954

Das Gehirn von *M. lamottei* unterscheidet sich vom durchschnittlichen Insektivoren-Gehirn vor allem durch geringer entwickelte olfaktorische Strukturen und eine größere Medulla oblongata. In der letzteren sind die Nuclei spinales nervi trigemini besonders stark vergrößert. Da sich ähnliche Merkmale bei allen wasserangepaßten Insektivoren, wie *Limnogale, Potamogale, Neomys, Desmana* und *Galemys* finden, wird ein Zusamm   .1hang mit der Nahrungssuche im Wasser angenommen. Das Trigeminus-System, welches die stark entwickelten Vibrissen der Oberlippe innerviert, scheint bei den wasserangepaßten Insektivoren das olfaktorische System als Hauptsinnessystem für die Nahrungssuche zu ersetzen.

Innerhalb der Otterspitzmäuse ist die Vergrößerung der Medulla oblongata und die gleichzeitige Reduktion der olfaktorischen Strukturen bei *M. lamottei* weniger stark ausgeprägt als bei *P. velox*. Dies wird mit Unterschieden in der Wasseranpassung in Zusammenhang gebracht.

In Merkmalen des Gehirns ähnelt *M. lamottei* am stärksten den spitzmausähnlichen Tenreks von Madagaskar (Oryzorictinae).

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